
IX.

A STUDY OF RESPIRATION IN ALCYONARIA.

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Although the respiration of many species of invertebrates has been studied in considerable detail, the only references to that of Alcyonaria which have come to the attention of the writer are those given by Montuori (1913), who studied two species, *Alcyomeum pallidum* and *Gorgonia cavolinii*. Two records only are given for each species, a small and a larger specimen having been compared in each case. In these experiments the total weight of the colony was taken as the basis of comparison without taking into account the proportion of inert skeletal material—the spicules in the first species and the spicules and chitinous axis in the latter.

Benedict (1915) has emphasized particularly the importance of the proportion of active protoplasmic tissue as shown even in the comparison of individuals of different sexes of the same species.

The observations herein recorded were made as part of a study of the ecological factors determining the distribution of Alcyonaria on the coral reefs of southern Florida. The data from which the amount of living tissue in the several species could be calculated were obtained three years ago in connection with a study of the importance of the alcyonaria as coral-forming organisms (Cary, 1915). A series of experiments were also carried out on the same species to determine their powers of resistance to increased temperature in order to discover whether or not there is any direct relationship between the rate of respiration and the temperature at which any species is killed; in other words, to determine whether the death of marine animals when subjected to high temperatures is in reality the result of asphyxiation, as Winterstein (1905) has maintained.

EXPERIMENTAL.

The respiration chambers consisted of museum jars, with clamped tops fitting on rubber gaskets. The capacity of the several jars varied from 960 c.c., to 1,250 c.c. as was determined by weighing each one empty and again when filled with distilled water at a known temperature. In all experiments with Alcyonaria the displacement of the specimen was determined and subtracted from the capacity of the jar. Frequently, when it was desired to make several determinations at intervals on the same specimen a fragment of coral rock was allowed to remain attached to the specimen in order to keep it upright during

the period between experiments, as these organisms quickly become abnormal if allowed to lie prone on their side on the bottom (Cary, 1914, p. 86). The specimens were kept in a live-car in the intervals between the experiments, so that their condition was normal, as was shown by the fact that the colonies would remain in good condition in this live-car for at least two months.

The sea-water for each series of experiments was brought fresh from the ocean in large aquarium jars and the respiration chambers were filled by submerging them in the large jars. The temperature was controlled by placing the respiration chambers in an aquarium containing about 75 liters of sea-water. This aquarium was covered with a black box to exclude the light, as some of the species studied contained within their tissues enough symbiotic algæ (*Zoöxanthellæ*) to materially influence the results when the experiments were carried on in the diffuse light of the laboratory. This thermostat was connected with the running-water supply of the laboratory and during a 2-hour experiment (the usual duration) the temperature would not vary more than 0.2° C. On unusually hot days, when the temperature of the ocean-water over the shallow reef flats was subject to marked fluctuations, it was found that a much more even as well as lower temperature was obtained by cutting off the water-supply to the tank, as the early morning temperature of the water would then be maintained within half a degree throughout the day, while the variation during the time of a single experiment would not be measurable with a thermometer reading to 0.2° C.

The oxygen in the water was determined by the Winkler method, using the precautions as regards the purity of reagents described by McClendon (1917*b*). Before taking the sample for analysis at the end of an experiment the respiration chamber was inverted several times to insure complete mixing of its contents. An extended series of comparisons showed that there was no detectable difference in the results obtained by drawing the water sample—250 c.c. through a glass siphon into the empty bottle or when siphoning into a bottle by the displacement of mercury (McClendon, *l. c.*). The former, less complicated and much more rapid, method was therefore followed. The hydrogen-ion concentration (P_{H}) of each fresh supply of water was determined by a colorimetric method and the amount of CO_2 which it contained calculated from the P_{H} and reserve alkali by a conversion table (McClendon, 1917*a*). In all the experiments it was found that so great a quantity of acid other than CO_2 was being given off that the values obtained for a respiratory quotient were far higher than would be obtained from the combustion of pure carbohydrates. Since the respiratory quotients were in every instance greater than unity, whatever the duration of the experiment, they have not been included in the table.

The results of all the experiments are summarized in table 1, in which the figures in columns 2 and 3 are the averages obtained from 5 determinations on specimens of various sizes of each species. *Briareum asbestum* has a central axis composed entirely of spicules, which in macerated specimens could not be certainly separated from those formerly contained in the cœnenchyma, so that both the skeletal masses are listed under the heading spicules.

TABLE I.

Species of Aleyonaria.	Percentage of spicules.	Percentage of chitinous axial skeleton.	Percentage of living tissues.	O ₂ consumed per kilogram of living tissue per hour.	Value of S/W.	Death temperature.
						°C.
<i>Briareum asbestum</i> ..	26.66	0.0	73.34	13.99125	3.25	38.2
<i>Eunecia crassa</i>	22.66	7.90	69.44	16.735	7.75	34.5
<i>Eunecia rousseaui</i> ...	35.60	11.28	53.12	20.75846	2.18	35.0
<i>Plexaura flexuosa</i> ...	30.66	5.10	64.24	16.6696	6.31	35.0
<i>Plexaura homomalla</i> ..	27.41	6.72	65.87	35.5878	5.82	35.0
<i>Pseudoplexaura crassa</i>	21.84	10.18	68.34	44.0062	5.90	34.5
<i>Plexaurella dichotoma</i>	35.86	7.57	56.57	18.585	2.72	35.0
<i>Plexaurella sp?</i>	24.95	4.45	70.63	35.7084	4.73	35.0
<i>Gorgonia flabellum</i> ..	22.33	11.75	65.92	74.5900	9.40	37.0
<i>Gorgonia acerosa</i> ...	19.75	7.08	73.17	54.9534	10.34	37.0
<i>Gorgonia citrina</i> ...	35.05	5.52	59.43	61.824	9.58	37.5
<i>Xiphigorgia anceps</i> ..	25.83	8.33	65.84	68.40	12.60	37.5

Five observations were made in each case.

DISCUSSION.

The validity of Rubner's (1885) hypothesis that heat-production (oxidation) is in direct proportion to the surface area of an organism has been denied by Montuori (1913) for all aquatic animals on the basis of his experiments recorded in that paper. On the other hand, Hoesslin (1888), Zuntz (1901), *et al.*, have maintained that their results on fishes support Rubner.

In *Aleyonaria* the surface in contact with the water varies greatly in different states of contraction or expansion of the colony. In the 12 species recorded in table 1 the surface area when expanded—all of them being able to completely retract their polyps—varied from 1.25 to 3.25 times that when the colony was in complete retraction. Since each species when undisturbed would arrive at complete expansion within a few moments after being put into the dark chamber, while on the other hand a slight agitation of the respiration chamber sufficed to cause them to remain contracted, the comparison of the consumption of oxygen under each of these conditions was a simple matter. While there were slight variations in the actual consumption of oxygen of any specimen in such a pair of experiments, the higher

metabolism occurred as frequently when the specimen had all its polyps completely withdrawn as when they were in full expansion.

Although the area of tissue exposed to the water had no constant effect on the rate of respiration, there was a striking relationship between the proportion of surface to weight of the several species and the rapidity of their respiration. As shown in column 6 of table 1, those species which have the greatest surface for a unit of weight ($\frac{\text{cm}^2}{\text{gms.}}$) have by far the highest metabolism. The areas used in these calculations were determined accurately for each specimen by measuring the length and the diameter of each branch of a colony and treating them as cylinders or cones according to their shape. Under the conditions necessarily imposed while making the measurements, the colonies were always in a state of complete contraction, so that, when the specimens were in full expansion, the values of S/W would be from 1.25 to 3.25 times greater than those recorded in the table.

RELATION BETWEEN DEATH TEMPERATURE AND RATE OF METABOLISM.

Column 7 of the table gives the temperatures found to be fatal to the different species on an exposure of 1 hour. When compared upon this basis the species studied fall into several groups; 2 of them succumb at 34.5° C.; another larger group finds the fatal temperature at 35° C., 2 others at 37° C., 2 at 37.5° C., while 1 species only could withstand temperatures up to 38.2° C. Although the last-mentioned species has the lowest respiration rate as well as the greatest power to withstand high temperature, there is no constant relationship between the death-temperature and the respiration-rate when all the species are compared. All of the species of the genus *Gorgonia* and the closely related *Xiphigorgia*, which have as a group the highest rate of respiration, are next to *Briareum* the most resistant to increased temperature. The two forms which are killed at the lowest temperature include *Eunecia crassa*, with next to the lowest rate of respiration, and *Pseudoplexaura crassa*, which stands eighth in the order of magnitude of respiration. Taken all together these observations offer no support to the hypothesis of Winterstein (1905), but on the contrary indicate that some other factor is the controlling agency in the ability of a marine organism to withstand high temperatures.

The heat experiments were performed in an open jar containing 6 liters of water and at the end of any experiment the amount of oxygen contained in the water was more than sufficient to allow respiration to go on in a normal manner if no other factor than oxygen tension were concerned. The acidity of the water at the close of the heat experiments was always greater than in respiration experiments carried on at 27.5° C. This may be only an expression of the abnormality of their metabolism at high temperatures, or have a causal relation to the death of the organism.

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